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Distribution and movements of fin whales in the North Pacific Ocean

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ABSTRACT

1. We summarize fin whale *Balaenoptera physalus* catch statistics, sighting data, mark recoveries and acoustics data. The annual cycle of most populations of fin whales had been thought to entail regular migrations between high-latitude summer feeding grounds and lower-latitude winter grounds. Here we present evidence of more complex and varied movement patterns.

2. During summer, fin whales range from the Chukchi Sea south to 35 °N on the Sanriku coast of Honshu, to the Subarctic Boundary (ca. 42 °N) in the western and central Pacific, and to 32 °N off the coast of California. Catches show concentrations in seven areas which we refer to as 'grounds', representing productive feeding areas.

3. During winter months, whales have been documented over a wide area from 60 °N south to 23 °N. Coastal whalers took them regularly in all winter months around Korea and Japan and they have been seen regularly in winter off southern California and northern Baja California. There are also numerous fin whale sightings and acoustic detections north of 40 °N during winter months. Calves are born during the winter, but there is little evidence for distinct calving areas.

4. Whales implanted with Discovery-type marks were killed in whaling operations, and location data from 198 marked whales demonstrate local site fidelity, consistent movements within and between the main summer grounds and long migrations from low-latitude winter grounds to high-latitude summer grounds.

5. The distributional data agree with immunogenetic and marking findings which suggest that the migratory population segregates into at least two demes with separate winter mating grounds: a western ground off the coast of Asia and an eastern one off the American coast. Members of the two demes probably mingle in the Bering Sea/Aleutian Islands area.

6. Prior research had suggested that there were at least two non-migratory stocks of fin whale: one in the East China Sea and another in the Gulf of California. There is equivocal evidence for the existence of additional non-migratory groups in the Sanriku-Hokkaido area off Japan and possibly the northern Sea of Japan, but this is based on small sample sizes.

Keywords: *Balaenoptera physalus*, discovery mark, migratory, resident, whaling

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INTRODUCTION

The fin whale *Balaenoptera physalus* is distributed nearly worldwide, and has discrete meta-populations in the North Atlantic, the North Pacific and the Southern Hemisphere (Mizroch, Rice & Breiwick, 1984). The distribution and population structure of fin whales in the North Pacific are rather poorly known. Fin whales were the targets of extensive commercial hunting in the 20th century, and they have been seen during many vessel and aerial surveys throughout the North Pacific; however, little information on their migratory patterns and possible stock separations has been summarized. In US marine mammal stock assessment documents produced by the National Marine Fisheries Service, Carretta *et al.* (2005) state that 'there is insufficient information to determine a population structure' for fin whales. Angliss & Lodge (2004) stated that fin whale stock structure is 'equivocal' and noted that, for conservative management purposes, three fin whale stocks are recognized: in the Northeast Pacific (Alaska), California-Oregon-Washington and Hawaii. The stock boundaries recognized by the International Whaling Commission (IWC) are very broad and were set in the absence of directed studies of fin whale stock identity in the North Pacific. For the purpose of setting catch limits only, the IWC recognized two stocks: in East China Sea and the rest of the North Pacific (Donovan, 1991).

In the North Pacific, fin whales range throughout the temperate and subarctic waters, including the Bering and southern Chukchi seas (Mizroch *et al.*, 1984). The distribution and movements of fin whales can be understood only with knowledge of their feeding ecology and reproductive patterns. Fin whales, like all baleen whales, are filter-feeders which depend upon food organisms such as euphausiids (krill) and small schooling fish that regularly aggregate into large swarms, schools or patches. Such patches are characterized by a high density of individuals, and in the North Pacific and other high-latitude regions occur mainly in the upper water layers less than 280 m from the surface (Brinton, 1962), although fin whales in the Mediterranean have been documented to dive to depths of at least 470 m (Panigada *et al.*, 1999).

It has been assumed by many observers that most populations of fin whales – like many species of baleen whales – adhere to a general seasonal pattern of migrating between high-latitude summer grounds and lower-latitude winter grounds (Mackintosh & Wheeler, 1929; Mackintosh, 1965). Specifically, Kellogg (1929) concluded that fin whales in the North Pacific migrated from Baja California to the Bering Sea. Annual migration may be related to the energetic advantages of calving in warmer and calmer seas (Kawamura, 1975), but this relationship is speculative and the reason for long-distance seasonal migrations in mysticetes remains unclear (see Corkeron & Connor, 1999; Clapham, 2001). Full-grown whales have sufficient insulation to maintain normal body temperature even in the coldest seas (Kanwisher & Sundnes, 1966), so there would seem to be little advantage in them migrating to lower latitudes. However, all whales must swim almost constantly in order to surface and breathe, so migrating to warmer waters costs little in terms of energy.

There is evidence of more complex and varied movement patterns of fin whales in the North Pacific. Kawakami & Ichihara (1958) hypothesized the existence of an 'American' stock and an 'Asian' stock based on Discovery-mark recovery data. Fujino (1960) suggested that there were multiple migratory stocks of fin whales based on immunogenetic data, i.e. the analysis of blood group antigens. He found that whales sampled in an area north of the Aleutians had consistent antigen groupings year to year, but whales sampled near Kamchatka and whales sampled south of the Aleutians showed inter-annual fluctuations in such groupings. He concluded that this fluctuation indicated that different stocks may have passed through the area (and been hunted there) at different times in the summer. Nishiwaki

(1966) also described two migratory stocks of fin whales: an eastern group and a western group, recognized by Discovery mark returns and 'serological means'.

Fujino (1960) suggested that whales caught in the East China Sea were part of a local population that did not migrate to northern waters. In addition to his immunogenetic findings, he analysed unpublished data which indicated that fin whales from the East China Sea were different from other North Pacific fin whales in terms of growth rate, length at sexual maturity, external body proportions, shape of skull and shape and growth rate of baleen.

Seasonality of sightings and genetic studies confirm that there is also a year-round resident population isolated in a peripheral sea in the Gulf of California (Tershy *et al.*, 1993; Bérubé *et al.*, 1998, 2002). Bérubé *et al.* (2002) analysed fin whale nuclear and mitochondrial DNA and demonstrated that these whales form an isolated population with a small effective population size. This is consistent with data from other ocean basins where some individuals and even some local populations, especially those in peripheral seas, do not follow a conventional migration schedule. Fin whales in the Mediterranean constitute a separate year-round non-migratory stock (Bérubé *et al.*, 1998; Canese *et al.*, 2006). In addition to populations that may follow conventional north-south migratory patterns in the North Atlantic, Jonsgård (1966) suggested that two separate populations of fin whales may feed in the waters near northern Norway: one during the early spring and the other during the summer months.

Here we add to these initial insights by reviewing a large body of available data on the distribution and movements of fin whales in the North Pacific Ocean. We first provide some background information on the species' prey, reproduction and life history. We then summarize data from catch records, opportunistic and directed sighting surveys, Discovery marking operations, and acoustics studies. By synthesizing these data, we summarize existing knowledge regarding North Pacific fin whale stock structure, as well as seasonal and migratory movements.

BACKGROUND TO THE SPECIES

Size and morphology

The fin whale is the second largest of all the whales, second in length only to the closely related blue whale *Balaenoptera musculus*. It is one of the Balaenopteridae, a family of mysticetes (baleen whales) whose members have fringed baleen plates in place of teeth. Balaenopterid whales, also known as rorquals, generally feed on swarms of small crustaceans or fish which they engulf by expanding their pleated throat grooves. They expel the water and the prey is caught in the fringes of the baleen plates.

Northern Hemisphere fin whales are somewhat smaller than their southern counterparts, and in all populations females are slightly larger than males. In the North Pacific, the largest female reported was 82 ft (25.0 m) and the average length (both sexes combined) was about 60 ft (18.3 m) (Mizroch & Rice, 2006). Among 357 females measured by Rice at whaling stations in California, the largest was 75 ft (22.9 m), and only three others exceeded 70 ft (21.3 m). In the Southern Hemisphere, Mackintosh (1942) noted that the largest fin whale reported in the International Whaling Statistics was an 88-ft (26.8 m) female. However, those length data are not entirely trustworthy and he noted that the largest reliably documented female was 85 ft (25.9 m), and that among the 996 females measured by the Discovery Committee staff, none exceeded 80 ft (24.4 m).

Morphologically, fin whales have a long, slender body form, and are sometimes said to be among the fastest of all the large balaenopterids. Because balaenopterid whales are fast swimmers and tend to sink when killed, most rorquals were unavailable to whalers until the

introduction of steam-powered catcher boats and the explosive harpoon in the late 1860s. As modern whaling spread from the North Atlantic in the late 19th century to the Antarctic and North Pacific in the early 20th century, whalers in some areas preferentially killed humpback whales *Megaptera novaeangliae* until they were commercially extinct, then turned to blue whales and fin whales (Tønnessen & Johnsen, 1982; Mizroch *et al.*, 1984). In the 20th century, fin whales were hunted in larger numbers than any other species (Mizroch, 1983); 720 000 were killed in the Southern Hemisphere alone (Clapham & Baker, 2002).

Prey and feeding

Fin whale prey species have been determined by analysis of stomach contents of whales captured during whaling. Therefore, knowledge of the prey species is limited by the seasonality and location of catches. Throughout the world, fin whales feed on euphausiids or 'krill' but they also consume substantial quantities of small nektonic fishes, at least locally and periodically (Nemoto & Kawamura, 1977).

Nemoto (1959) analysed stomach contents data from 7505 fin whales killed between 1952 and 1958 in the northern part of the North Pacific and Bering Sea. Over that time span, he noted major variations in prey types and prey distributions, but in most cases, euphausiids were the most common foods in the Aleutians and the Gulf of Alaska, and schooling fishes predominated in the northern Bering Sea and off Kamchatka.

Fish was the main food reported for fin whales north of 58 °N in the Bering Sea, mainly capelin *Mallotus villosus*, Alaska pollock *Theragra chalcogramma* and Pacific herring *Clupea pallasi*. Alaska pollock was also most common along the northern Bering Sea shelf edge. In the northern Bering Sea, *Thysanoessa raschii* was the only species of euphausiid taken by fin whales (Nemoto, 1959). Herring appeared to be the main food for fin whales along the Kamchatka coast of Russia (Zenkovich, 1934) and fin whales were called 'herring whales' by the early Russian whalers (Zenkovich, 1954).

Sometimes the euphausiid *T. raschii* was taken together with capelin in the Gulf of Anadyr and Cape Navarin areas on the edge of the northwestern Bering Sea. In areas where the copepod *Neocalanus cristatus* was abundant, such as around the Aleutians and in Olyutorsky Bay off northeast Kamchatka, fin whales were found to take large quantities of this species (Nemoto, 1959).

The fish consumed by fin whales in Arctic and subarctic waters were mainly capelin, walleye pollock, Pacific herring and (in the northern Bering Sea only) saffron cod *Eleginus gracilis* [Andriyashev, 1954 (1964 translation), 1955; Miller & Schmidtke, 1956; Hourston & Haegele, 1980; Frost & Lowry, 1986; Krieger, 1990]. All of these fish are small, mainly between 10 and 30 cm in length.

In the Kuril Islands region (southwest of Kamchatka and northeast of Japan), the prey of 234 fin whales was examined from 1951 and in the period 1953–56 (Betesheva, 1961). Prey species varied greatly year to year and there was some evidence of regional differences in prey between the northern Kuril Islands and the southern areas. In the northern area, prey was mostly zooplankton such as krill (*T. longipes, T. inermis and T. raschii*) and *Neocalanus* copepods (*N. plumchrus* and *N. cristatus*). In the southern areas, squid *Todarodes pacificus pacificus* and small schooling fish such as Pacific saury *Cololabis saira* and Japanese anchovy *Engraulis japonicus* dominated.

In the Subarctic waters around the Aleutian Islands and in the Gulf of Alaska, five species of krill were the predominant prey in the stomachs of animals killed during Japanese whaling: *Euphausia pacifica*, *T. spinifera*, *T. inermis*, *T. raschii* and *T. longipes* (Nemoto & Kasuya, 1965).

In the waters off the Canadian west coast, the prey of fin whales processed at the Coal Harbor whaling station from 1963 to 1967 was predominantly 'euphausiids' (not identified to species level), although in 1964 and 1965, copepods made up 13 and 37% of the diet, respectively (Flinn *et al.*, 2002). To the south in the cool California Current, only two euphausiid species – *E. pacifica* and *T. spinifera* – were recorded as food for fin whales caught between 1959 and 1970 (Rice, 1977). Anchovies *Engraulis mordax* were the only species of fish regularly eaten by fin whales during the final years of whaling off California (1959–70; Rice, unpublished data), but sardines *Sardinops sagax* were probably taken before their population collapsed in the 1940s and 1950s. Both species congregate in large, dense schools in the epipelagic zone, and they are also among the most dominant species, at least locally, in terms of biomass.

In the Gulf of California (Mexico), *Nyctiphanes simplex* was the dominant species in the diet of fin whales (Tershy, 1992). All of the species of krill eaten by fin whales are abundant, gather in dense swarms and live near the water surface, which makes them both vulnerable to predation by baleen whales and an energetically profitable food source (Brinton, 1962; Mauchline & Fisher, 1969; Brinton, 1976; Mauchline, 1980).

Almost all of the main prey species of fin whales reach their greatest abundance in near-surface waters during the summer months, and in the highly productive areas of cooler waters found in higher latitudes and in eastern boundary currents. Therefore, the whales aggregate during summer in these areas, where they feed heavily. During the winter when food is sparse, the whales generally disperse to mostly unknown destinations where it has been assumed they fast or feed very little (Brodie, 1975).

Reproduction and life history

Based on data from Antarctic populations, the 2-year breeding cycle of the fin whale appears to be synchronized with its annual migrations and feeding (Mackintosh & Wheeler, 1929; Mackintosh, 1942, 1965, 1966; Laws, 1961; Brown & Lockyer, 1984). Fin whales have traditionally been assumed to mate in the winter in lower latitudes, and then migrate back to their high-latitude summer feeding grounds. At the end of a gestation period of about 1 year, it has been assumed that the female gives birth to a single calf on or near the winter grounds, but since sightings on the winter grounds are rare this has never been confirmed. In the spring, mothers take their calves to the feeding grounds, fidelity to which appears to be maternally directed (Clapham & Seipt, 1991). Calves are probably weaned sometime before the end of summer or autumn. The complete breeding cycle thus occupies between 1.5 and 2 years, and the majority of females calve at 2-year intervals (Agler *et al.*, 1993). Data from fin whales landed at California whaling stations from 1958 to 1970 indicated that the mean annual incidence of pregnancy among sexually mature females was 36% (Rice, unpublished data).

As noted previously, there is some evidence to question the traditional assumption of a strict seasonal migration in fin whales, for at least some populations.

DATA SOURCES

During the 1960s and early 1970s, national whale research projects throughout the North Pacific were coordinated by the North Pacific Working Group (NPWG), which was appointed by the Scientific Committee of the IWC. The NPWG consisted of four members, one each from the Fisheries Research Board of Canada (FRBC), the Whales Research Institute (WRI) in Japan, the All-Union Research Institute for Marine Fisheries and Oceanography (VNIRO) in the USSR, and the United States Fish and Wildlife Service's Marine Mammal Biological Laboratory [precursor of the National Oceanic and Atmospheric

Administration's (NOAA) National Marine Fisheries Service's National Marine Mammal Laboratory (NMML)]. The NPWG developed standard formats for recording data and exchanged among themselves information on catches, effort, sightings and basic biological parameters such as age, sex and reproductive status. Although not part of the NPWG, the Instituto Nacional de Investigaciones Biologico Pesqueras (INIBP) in Mexico collaborated in some of the marking and sighting cruises. Data from the NPWG were used in a number of the papers cited here and form the basis for much of our review.

We used four sources of data in our analysis of fin whale distribution and movements: (i) catch statistics; (ii) sighting data; (iii) recoveries of whales marked for individual identification; and (iv) acoustics data from offshore hydrophone arrays developed by the US Navy. Details of each of these sources are provided in the subsequent sections.

Catch statistics

Fin whales were killed in the North Pacific by various nations until 1985; catches by nation and time period are summarized in Table 1. Such catch statistics are an extensive source of data on whale distribution because of their great volume, broad geographical scope and continuous coverage over many decades. These data were archived by the Bureau of International Whaling Statistics (BIWS) in Sandefjord, Norway. By 1981, these duties had been transferred to the IWC in Cambridge, UK. Additional catch records were available for the Japanese floating factory *Tonan Maru*, obtained by the Supreme Commander for the Allied Powers for the 1940 operations. These *Tonan Maru* statistics are important because they cover the only periods when modern-style whaling was conducted north of the Bering Strait.

There were 49 936 reported fin whales kills in the North Pacific during the years 1911 to 1985 (C. Allison, pers. comm. BIWS/IWC Summary Catch Database Version 3.5, distributed on 11 February 2008). Reported catches of fin whales by each whaling nation are shown in Appendix S1. Of these, 48 040 records included information on date, location (latitude and longitude), body length and sex. There were 38 623 records with latitude and longitude reported to the nearest degree and minute, 1072 records with latitude and longitude reported to the nearest degree or half degree and 8574 records with latitude and longitude estimates. There were 1896 records with no latitude or longitude recorded at all, mainly from catches reported by the USSR in the 1960s.

After the end of the Cold War in the early 1990s, Russian and Ukrainian biologists were able to reveal the original catch records for Soviet whaling fleets, which conducted a massive campaign of illegal whaling worldwide (including the North Pacific) from 1947 to 1972 (Yablokov, 1994; Yablokov & Zemsky, 2000). These records revealed wholesale falsification of catch data submitted by the USSR to the IWC, including over-reporting of some species to cover up illegal catches of other, protected species (see also Ivashchenko, Clapham & Brownell, 2006). The Soviet catch of fin whales in the North Pacific was under-reported in 1963 and 1964, and over-reported from 1965 to 1967. By 1968, the catch of fin whales, though still over-reported, was at a much lower level (Doroshenko, 2000), but no locality information was reported for the 1064 kills reported as fin whales in 1968 (see Appendix S1).

Because the correct Soviet catch data are not in the IWC database, we have omitted all Soviet catches reported as fin whales during the years 1963–68 from the figures plotted here. Omitting these data does not change the overall pattern of seasonal concentrations and zones of high density, and ensures that whales other than fin whales are not shown on the distribution maps. For example, during the 1965–67 period when fin whale catches were over-reported, some whales were caught (and reported as fin whales) much further south than most

Table 1. Annual catches of fin whales in the different whaling grounds, excluding the questionable Soviet data from the years 1963–1967

Year	East China sea	Sanriku Hokkaido	Kamchatka/w. Bering Sea/w. Aleutians	E. Bering Sea/e. Aleutians	Gulf of Alaska	Vancouver	California and Mexico	Total
1911					208			208
1912					187			187
1913					73			73
1914					88			88
1915					64			64
1916					82			82
1917						39		39
1918					50	69		119
1919					42	64		106
1924				148				148
1925			153	235			1	389
1926			214	197	5			416
1927				85	21		1	107
1928				52	47		1	100
1929	152	216		79	26		1	474
1930				28	21			49
1932					60			60
1933					61			61
1934				156	78			234
1935			150	117	32	20	3	322
1936				107	50			157
1937					170		14	184
1938				66	1	49		116
1939				91				91
1946	7	226						233
1947	15	242				17		274
1948	18	161				56		235
1949	1	269	56			115		441
1950		248	73	18		150		489
1951		381	75			225		681
1952	22	450	447			240		1 159
1953	12	416	607			181		1 216
1954		463	802	752		150		2 167
1955	226	362	212	1 212		120		2 132
1956	277	319	652	820		167	3	2 238
1957	186	251	381	1 101		284	22	2 225
1958	172	378	474	896		574	108	2 602
1959	80	270	795	787		372	108	2 412
1960	20	376	332	1 166	23		138	2 055
1961	9	218	201	905	425		118	1 876
1962		116	6	573	587	158	123	1 563
1963		67		8	1037	225	16	1 353
1964	64	56	55	223	701	169	147	1 415
1965		71	30	634	692	134	113	1 674
1966	19	85	165	336	765	134	42	1 546
1967	18	77	727	83	34	102	44	1 085
1968		53	484	184	61		38	820
1969		83	399	468	205	90	31	1 276
1970		104	269	258	219	146	16	1 012
1971		77	322	239	138	19	4	799
1972	34	55	419	25	70	155		758
1973	14	56	113	26	127	107	17	460
1974	2	36	76	1	129	147	22	413
1975		11	48	2	52	43	6	162
1980	4							4
1985	1							1
Total	1353	6193	8737	12 078	6631	4521	1137	40 650

of the other fin whales. These purported fin whales were caught in areas of high sperm whale *Physeter macrocephalus* catches, and were probably the latter species.

In summary, the catch data analysed in this paper include 40 650 catch records with length and locality information reported for fin whales caught between 1911 and 1985 (Table 1). This total excludes 7390 questionable Soviet records for the years 1963 to 1967.

Commercial whaling operations fell into two categories, coastal and pelagic. These are described further in the subsequent sections.

Coastal whaling

Coastal whaling includes whaling operations carried out from shore-based stations, as well as operations from old-style factory ships. Reeves & Smith (2006) classified the latter operations in their category Factory Ship Whaling, together with the modern factory ships which had stern slipways for hauling whales on deck and which operated on the high seas. However, we consider this classification inappropriate: the old-style factory ships lacked slipways, so the whales were flensed in the water alongside the vessel. Of necessity they operated from protected anchorages along the coast, in essentially the same fashion as shore stations.

From 1905 to 1971 there were many such whaling operations along the western coasts of North America, from Akutan in the eastern Aleutian Islands south to Bahia Banderas in the state of Jalisco, Mexico. North of 35 °N, this coastal whaling was almost entirely a summer fishery, operating between 1 May and 31 October (or from 16 April to 15 October at the central California stations from 1960 to 1968). The fishery off Mexico was prosecuted mainly in the winter, from December to May, but was occasionally extended from October to July.

Rice (unpublished data) has compiled catch records and, where available, effort data for almost all of these coastal operations (Appendix S2). Reeves *et al.* (1985) summarized whaling results for pre-World War 2 catches at Akutan (1912–39) and Port Hobron (1926–37) in Alaska. Gregr *et al.* (2000) summarized pre- and post-war results from the Canadian whaling stations. Clapham *et al.* (1997) published detailed catch records from the California shore stations from 1919 to 1926. From Alaska south to California, the catch was predominantly fin and humpback whales. In Mexico, however, only 12 fin whales were taken, all from December to June; the major targets there were humpback and blue whales. The effect of these pre-war (1905–40) catches on the whale populations has not been quantified, but it was probably great enough at least to reduce somewhat the numbers of fin whales in the eastern North Pacific prior to the advent of large-scale pelagic whaling.

On the western side of the North Pacific, Japan had a centuries-old history of old-style whaling (Kasuya, 2002). Modern-style shore station whaling using catcher-boats with harpoon cannons was introduced to Japan in 1899, and it soon spread widely. Whaling by Japanese companies from 1911 to 1949 was summarized by Kasahara (1950) (see Appendix S3). A total of 83 different shore stations operated at various times in this period. They were spread from Paramushir (50 °N), the northernmost of the Kuril Islands, south to Taiwan (23 °N) and the Ogasawara (Bonin) Islands (27 °N). Kasahara (1950) classified Japanese whaling grounds into 16 areas, and presented total annual catches for each of these areas. Mizue (1950) also presented total annual catches for all of these areas combined (Appendix S4). The numbers published by Kasahara and Mizue are in fairly close agreement for 1922 to 1937, but for the earlier years (1911 to 1921), many of Mizue's figures are much higher than Kasahara's. This can be explained by the fact that there were many missing data (indicated by '?') in Kasahara's tabulation, so we have accepted Mizue's figures as the more accurate ones. Mizue (1950) plotted the catch position of each whale on a series of 12 monthly maps.

Most of these early Japanese catches have not been incorporated in the BIWS database, and we have not located any further data, such as sex and body length, on them.

Kondo & Kasuya (2002) noted that some Japanese shore station catches of fin whales had been under-reported to the BIWS and they provided corrected statistics for shore stations operated by the Nihon Kinkai Hogei Company from 1965 to 1978. They noted that fin whale catches were generally under-reported for shore stations off the northern coast of Hokkaido (Mombetsu) and the eastern coast of Hokkaido in the northern Sea of Japan (Wakkanai).

Also in the western North Pacific, a Russian company established a shore station at Hajdamak, 180 km east of Vladivostok, in 1889, but it closed in 1890 after its catcher-boat was lost at sea. The station was reopened by another company in 1895 and operated until 1901, when it was destroyed by fire. In 1899, the same company converted a vessel into a floating factory, the *Michail*; whaling commenced in 1903 but was brought to a halt in 1904 by the Russo-Japanese war (Berzin, 2008). Details of Russian catches in these early years are unavailable.

After the Second World War, jurisdiction over the Kuril Islands was transferred from Japan to the Soviet Union. In 1948, the government reopened five of the former Japanese whaling stations. These were Podgorniy on Paramushir I., Skalistiy on Simushir I., Yasniy and Kasatka on Iturup I., and Ostrovhoy on Shikotan I. The stations on Simushir and Shikotan closed after the 1961 season, the other three after 1964. Catch reports from all five were submitted to the BIWS.

Pelagic whaling

Modern-style harpoon-cannon whaling on the high seas was made possible when whalers working off South Orkney in the Antarctic invented the stern slipway during the 1912/13 whaling season, although purpose-built stern-slip factory ships did not appear until 1925 (Hart, 2006). Prior to the end of World War II, two pelagic whaling fleets operated in the North Pacific (Tønnessen & Johnsen, 1982).

The Soviet floating factory *Aleut* was the first factory ship with a stern slipway to operate in the North Pacific. In 1933, the *Aleut* (then on her maiden voyage) and her fleet of three catcher-boats hunted whales while crossing the Pacific from Mexico to Vladivostok (Zenkovich, 1954). In subsequent years, until 1972, this fleet operated every summer in the western North Pacific from the Kuril Islands to the Chukchi Sea. Catch data for the years 1933 to 1935 were published by Tomilin (1937a); data for other years for the *Aleut* fleet are available from the IWC, although their reliability remains to be determined.

Pelagic whaling was suspended during World War II, except, as noted previously, by the *Aleut*, which operated every year, and the Japanese floating factory *Tonan Maru*, which operated in 1940 and 1941 (Kasuya, 2002). Mizroch & Rice (2006) detail the development of post-World War II pelagic whaling, and describe the expansion of whaling starting in 1946. From 1946 to 1951, whaling occurred mainly around Japan, the Kuril Islands and in the Bering Sea near Kamchatka.

Starting in 1947, pelagic whaling for baleen whales was restricted by the IWC to the 6-month season from May to October, and was limited to waters north of 20 °N in the western and central Pacific (west of 150 °W) and north of 35 °N in the eastern Pacific. North of the Bering Strait, whaling was allowed north to 72 °N in the sector between 150 °E and 140 °W. In this paper, we therefore broadly describe the observational effort involved in the pelagic catch records for the post-war period.

Beginning in 1952, the number of Japanese and Soviet factory ships working in the North Pacific began to increase and whaling expanded geographically to include the central Bering

Sea, Aleutian Islands, and a small amount of whaling in the Gulf of Alaska. During the peak years from 1963 to 1967, six pelagic fleets (three Japanese, three Soviet) were hunting baleen whales throughout the North Pacific. After the 1975 season, the IWC banned the killing of fin whales in all oceans.

Sighting data

Sighting data are much less extensive than catch data. Most sighting or census cruises are geographically limited, and many are one-time events. Unless a cruise is specifically dedicated to cetacean research, any sighting data obtained are difficult to quantify. Nevertheless, for many times and places, sighting records are the only data available.

Japanese sighting data

Japanese sighting data, which represent the most extensive body of sighting information available for the North Pacific, come from two sources. The first is data from the dedicated scouting vessels that operated throughout the North Pacific pelagic whaling grounds from 1964 to 1988. Because these vessels were attached to the whaling fleets, their temporal and geographical coverage largely paralleled that of those fleets. Methods were described by Ohsumi & Yamamura (1982). Because the vessel tracklines were not developed using line-transect methods and because perpendicular sightings distances cannot be computed from the data collected, the data do not allow the estimation of abundance, but they are useful to show seasonal distribution in the areas and seasons in which whalers operated.

Other sightings were made from research vessels chartered by the Japanese Fisheries Agency from 1972 to 1990. From the scouting vessel data, Wada (1981) calculated an 'Index of Abundance' by 10-degree squares of latitude and longitude by year, all months combined. Miyashita, Kato & Kasuya (1995) combined the data from the scouting vessels and the research vessel data, and summarized them as sightings per mile by 5-degree squares by month, all years combined. It is not possible to estimate actual numbers from this type of dataset, but the summary is very useful to show overall seasonal distribution of whales throughout the North Pacific (and other areas).

Platforms of Opportunity Program (POP)

The NOAA POP was initiated in 1975 as part of an environmental assessment programme conducted in Alaskan waters (Mercer, Krogman & Sonntag, 1978); the resulting data are managed by staff at NMML.[1] The programme has received both opportunistic and directed marine mammal sighting data, primarily reported by personnel on vessels operating in the North Pacific. The database also contains records dating back to 1958 that were collected as part of pelagic studies conducted by NMML personnel.

POP sighting data are opportunistically collected on NOAA, Navy, US Coast Guard and some fishing and tourist boats. Observer effort is dependent upon the interest of the observers and on their workload. POP data cannot be used to infer abundance, or even indices of abundance, and apparent gaps in distributions could just be an absence of sighting effort in certain areas. Sighting data are evaluated by trained data editors and species identifications are considered to be 'confirmed' only if the observer has described a plausible suite of sighting cues or provided other associated data (sketches, behavioral notes, etc.). Unconfirmed sightings were not used in this analysis.

[1]Data available upon request: National Marine Mammal Laboratory, 7600 Sand Point Way NE, Seattle, WA 98115, USA.

The POP database contains records of 1488 confirmed fin whale sightings during the period 1958–2000 (Appendix S5). Fin whales were seen in all months of the year.

Dale W. Rice, unpublished data

Sightings of 92 fin whales were recorded during 30 whale research cruises from 1958 to 1980 (Appendix S5). Data from these cruises covered the Eastern Pacific from the northern Gulf of Alaska (60 °N) south to 12 °S, and west to the Leeward (northwestern) Hawaiian Islands.

Additional sighting data

Additional sighting data include sightings of fin whales collected opportunistically by various observers (eight sightings), by personnel at the Kodiak National Wildlife Refuge, Kodiak Island, Alaska, USA from February to April during the years 1980–2001 (200 sightings), directed cetacean aerial surveys conducted in the Bering Sea in July each year from 1998 to 2000 by personnel from the Southwest Fisheries Science Center, La Jolla, California, USA (228 sightings), and directed cetacean aerial surveys conducted in the Gulf of Alaska in June–July 1998 and 2000 by personnel from NMML (95 sightings; Appendix S5).

In addition, fin whale sightings were taken from reports of research cruises conducted off the US West coast (Forney & Barlow, 1993, 1998; Barlow, 1994, 1995; Forney, Barlow & Carretta, 1995; Barlow & Gerrodette, 1996). Fin whale sightings in the Bering Sea were summarized by Moore *et al.* (2002). Fin whale sightings off western Alaska and the central Aleutians were summarized by Moore *et al.* (2002). Zerbini *et al.* (2006) presented an abundance estimate of 1652 (95% CI: 1142–2389) and an estimated rate of increase of 4.8% (95% CI: 4.1–5.4%) for a small portion of the fin whale's range in the North Pacific.

Recoveries of marked whales

Extensive whale-marking programmes were undertaken by research groups from Japan (Omura & Ohsumi, 1964; Ohsumi & Masaki, 1975) and the Soviet Union (Ivashin & Rovnin, 1967). These research groups all used Discovery-type marks for tagging whales. The Discovery-type mark is a uniquely numbered steel tube 24-cm long tipped with a conical lead point 38-mm long. It was fired from a 12-gauge shotgun, propelled by a shotgun shell (lacking lead pellets). See Rayner (1940) for a description of the evolution of the Discovery mark and Brown (1977) for a review of the marking programmes. When properly implanted, it is completely buried in the blubber or muscle, and can be recovered only when the whale carcass is flensed; the unique number of each mark provided information on the locations of marking and recovery to be recorded. The number of whales marked with Discovery marks in each whaling area by national whaling fleet is shown in Table 2.

Japanese researchers marked a total of 866 fin whales from 1949 to 1972. Japanese whale marking was conducted in the northern Sea of Japan, the Sanriku-Hokkaido area, the Kamchatka-western Aleutians grounds, the Bering Sea-eastern Aleutians grounds, the Gulf of Alaska, and the Vancouver grounds, with the majority of the marks placed in the Bering Sea-eastern Aleutians and Gulf of Alaska.

According to Ivashin & Rovnin (1967), Soviet researchers marked a total of 51 fin whales from 1954 to 1966, although they account for only 43 fin whale marking events in their detailed tables of marks placed in each area by Soviet researchers, and they provide no explanation for the discrepancy; consequently, we used the number 43 when summarizing marks by area placed. Soviet whale marking was conducted near Kamchatka, in the Bering Sea, in the Gulf of Alaska, off Vancouver Island, off California, and in some other areas south of the major whaling grounds.

Table 2. Number of fin whale marks and recoveries in each whaling area by each nation

Area marked	Japan (1949–72)	USSR (1954–66)	USA (1962–69)	Total marked	Total recovered	Percent recovered
US and Canadian West Coast (II B)	31	3		34	6	18%
Gulf of Alaska (Yakutat to Alaska Peninsula) (III B)	182	6		188	45	24%
Eastern Bering Sea (IV A)	436	10		446	114	26%
South of Aleutians (160 °W-180) (IV B)	104	3		107	16	15%
Western Bering Sea (V A)	34	5		39	7	18%
South of Aleutians (180-160 °E) (V B)	53	3		56	9	16%
Sea of Okhotsk (VI A)	4	1		5	3	60%
Sanriku-Hokkaido (VI B)	19	2		21	2	10%
Sea of Japan (VII A)	2	0		2	1	50%
South of main whaling areas (VI C)	1	0		1		0
California and Baja California			56	56	11	20%
Other areas		10		10	0	0
Total	866	43*	56	899	214	24%

*Soviet researchers marked a total of 51 fin whales from 1954 to 1966, but they account for only 43 fin whale marking events in their detailed tables of marks placed by area.

The US Marine Mammal Biological Laboratory conducted a programme of tagging whales with Discovery marks from 1962 to 1969. Because most whaling operations in the eastern North Pacific were conducted between April and October, marking efforts were concentrated during the winter in low-latitude waters, mainly between 20 °N and 37 °N, in hope of providing evidence that would connect rorqual populations on the winter grounds with the stocks that were being exploited on the summer feeding grounds. In total, 56 fin whales were marked by members of US expeditions (Table 2).

Acoustics data

Thompson & Friedl (1982) monitored whale vocalizations received by two fixed underwater hydrophones moored near the northernmost point of Oahu in the Hawai'ian archipelago. Moore *et al.* (1998) and Watkins *et al.* (2000) analysed data on fin whale vocalizations received by sea bed-mounted and sound channel-mounted offshore hydrophone arrays. These arrays were deployed in much of the North Pacific between 25 °N and 55 °N by the US Navy Sound Surveillance System (SOSUS) (Wit, 1981; Richelson, 1998). Although the SOSUS system was created for military purposes, it regularly recorded fin and other whales, and in recent years these data have been made available to selected researchers. Stafford *et al.* (2007) analysed data from six Sound Fixing and Ranging (SOFAR) channel moored hydrophones deployed in the Gulf of Alaska.

RESULTS AND DISCUSSION

General distribution and movements

The geographical distribution of the total catches for all years combined (Fig. 1) show seven areas of great numbers of fin whale catches, which we will refer to as 'historical whaling grounds'. For further analysis, we delimit these grounds as follows, from west to east:

East China Sea Ground (120 °E to <135 °E).

Sanriku Hokkaido Ground (135 °E to <155 °E).

Kamchatka/western Bering Sea/western Aleutian Ground (155 °E to <180°).

Eastern Bering Sea-eastern Aleutian Ground (180° to 160 °W).

Gulf of Alaska Ground (<160 °W to 135 °W); this was called the 'Northwest Coast Ground,' which includes the 'Kodiak Ground'.

Vancouver Ground (<135 °W to 125 °W).

California and Mexico Ground (<125 °W to 100 °W); this includes the Farallon Ground off central California and a few catches in the Pacific off Baja California.

In addition, there is a Gulf of California Ground (20 °N to 30 °N inside the gulf) which is inhabited by a fin whale population that, based on seasonal observations and genetics studies, appears to be isolated (Tershy *et al.*, 1993; Bérubé *et al.*, 1998, 2002), but no whaling for fin whales was ever conducted in the Gulf.

Combining data from all years reveals general geographical patterns, but conceals any year-to-year variations in whale or whaling distribution. The annual catch totals on each ground for each year from 1911 to 1985 (Table 1) show that there is considerable variation

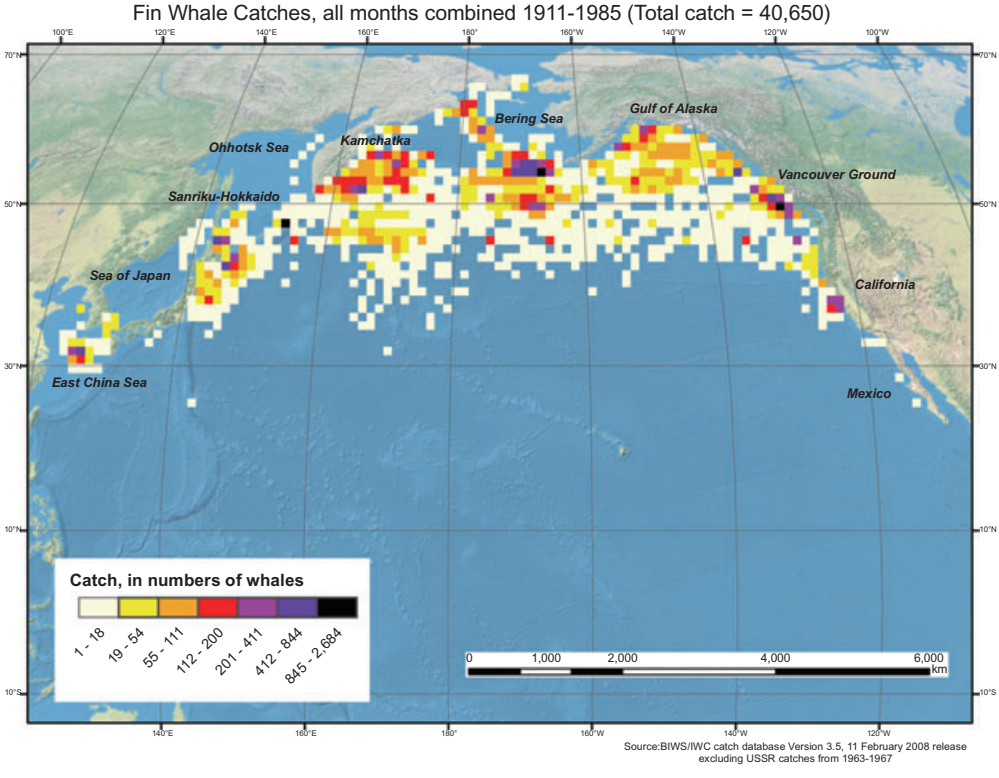


Fig. 1. Fin whale catch distribution by historical whaling ground, summed by 1° × 1° square.

from year to year, which could be due in part to the distribution of the whaling fleets (the catch effort) as well as the distribution of whales. The pattern of fluctuations of whale densities may differ between grounds.

To simplify our analysis of the distributional data, we divide the year into two seasons. 'Summer' (May to October inclusive) encompasses the months during which the extensive postwar pelagic whale fishery was conducted, as well as the numerous coastal whaling operations from 1905 to 1971 (Fig. 2a–f). 'Winter' (November to April inclusive) includes the months during which almost no pelagic whaling occurred; in the western North Pacific, there was a substantial long-term winter fishery for fin whales in coastal waters of Japan and Korea. The only winter fishery in the eastern North Pacific was that along the coast of Mexico, but very few fin whales were caught.

Summer range

The most extensive dataset showing the distribution and numbers of whales on the summer grounds are the catch statistics (Fig. 2a–f). We produced catch maps that show monthly concentrations of whale catches using shaded density grids categorized using the 'natural breaks' algorithm (Jenks, 1963) within the program ArcMap 9.2. The Jenks algorithm groups similar values and selects break points based on natural groupings within each dataset. Because each catch map represents a different subset of the catch database, each density grouping gives the optimal class breaks for total catches within that month's dataset.

The pelagic whaling fleets naturally centred the bulk of their hunting effort in those areas and months where experience had shown that higher densities of whales might be expected, although whaling would have been difficult or impossible in the winter months in northern Arctic waters due to the inclement weather and ice. Because of these operational guidelines, raw catch numbers tend to exaggerate the temporal and spatial patterns of whale distribution, but remain the most comprehensive source of data on historical whale densities and distribution.

Northern limits

During the summer, fin whales are found throughout the entire subarctic North Pacific (Fig. 2a–f). To the north, they range into the southern Sea of Okhotsk, the Bering Sea and the northern Gulf of Alaska. They pass through the Bering Strait into the southwestern Chukchi Sea during August and September. Many were taken as far west as Mys (Cape) Shmidta (68°55′N, 179°24′E), and as far north as 69°04′N, 171°06′W, by the *Aleut* fleet from 1933 to 1935, and by the *Tonan Maru* fleet in 1940.

Zenkovich (1934, 1938a), a biologist who worked aboard the *Aleut* from 1933 to 1936, reported that 'The Polar Sea, in areas near Cape Dezhnev which we visited, is frequented by large schools (literally hundreds of animals) of fin whales, humpbacks, and grays'. He further described (Zenkovich, 1938b) how the fin whales were '. . . encountered from early spring to the beginning of winter in groups of from 2 to 3 up to 10 individuals, mostly at a distance of 10 to 30 miles (16–50 km) from shore, but sometimes very near the shore (Seniavin Strait)'. Similar accounts were published by Tomilin (1937a,b), another biologist assigned to the *Aleut* fleet, who noted that 'Cape Schmidt was the extreme western point where fin whales were observed in the Chukchi Sea in 1934' (Tomilin, 1957). Nikulin (1946), who conducted observations from points along the coasts around the Chukotski Peninsula between 1937 and 1941, counted 336 fin whales from July to October; he said that the species '. . . is found in groups in the Chukchi area from the second half of June to the end of October'. Sleptsov (1961), in a comprehensive review of the status of cetaceans in the Chukchi Sea, described the

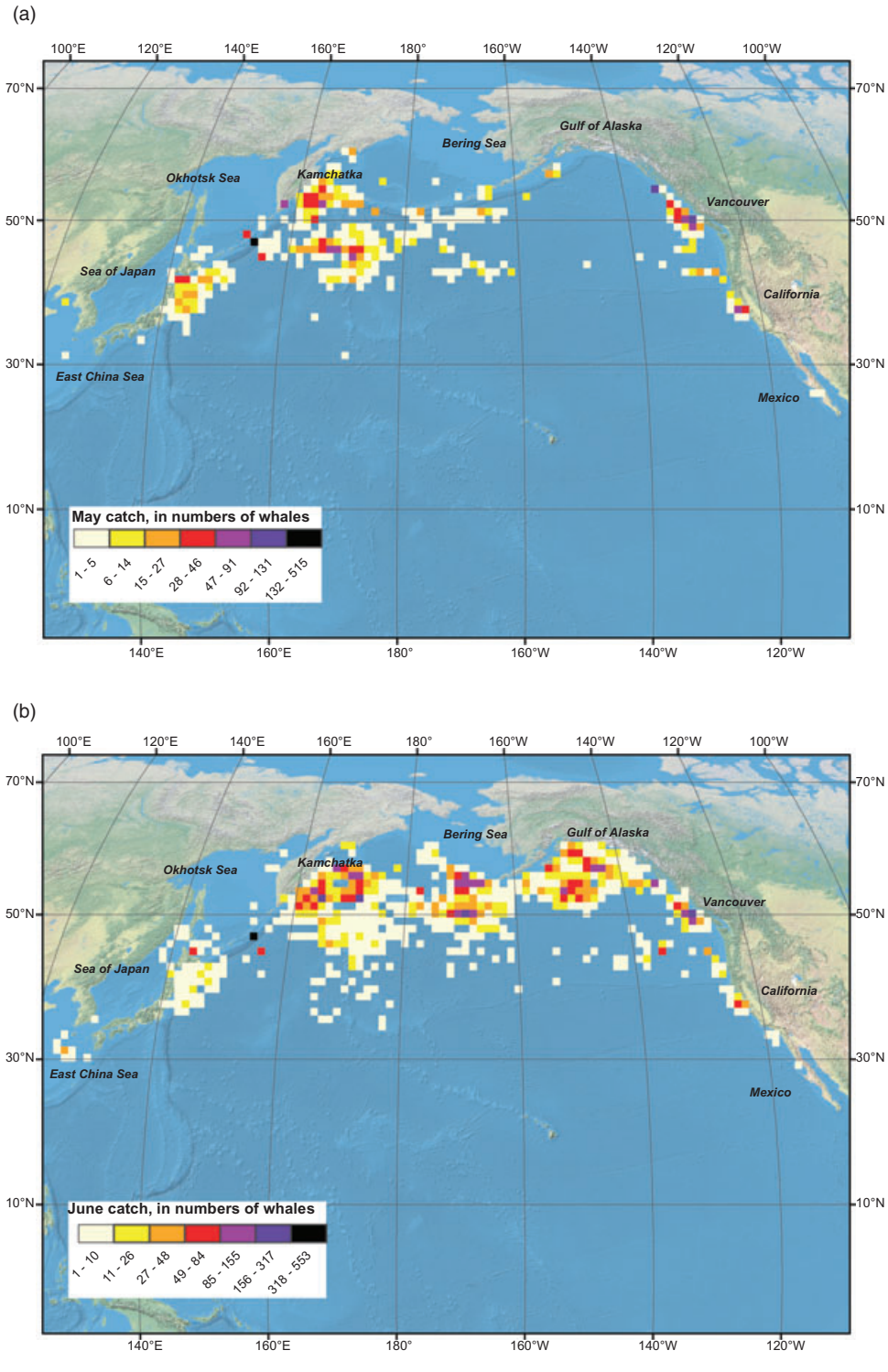
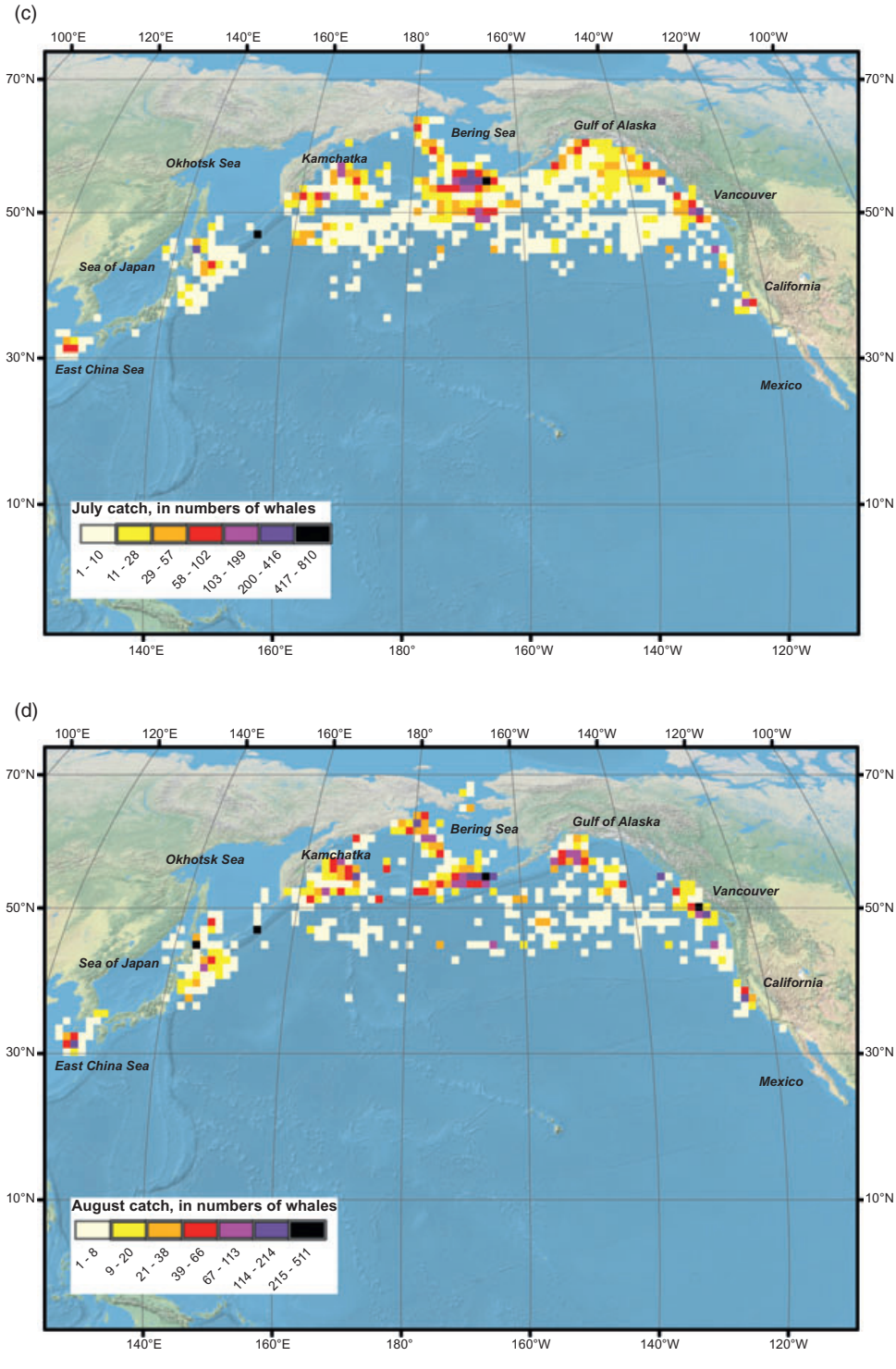


Fig. 2. Fin whale catches from 1911 to 1985, summed by 1° × 1° square (panel). (a) May (n = 3490). (b) June (n = 10 204). (c) July (n = 12 854). (d) August (n = 8640). (e) September (n = 3529). (f) October (n = 1210). Source: BIWS/IWC catch database, version 3.5, 11 February 2008 release, excluding USSR catches from 1963–1967.



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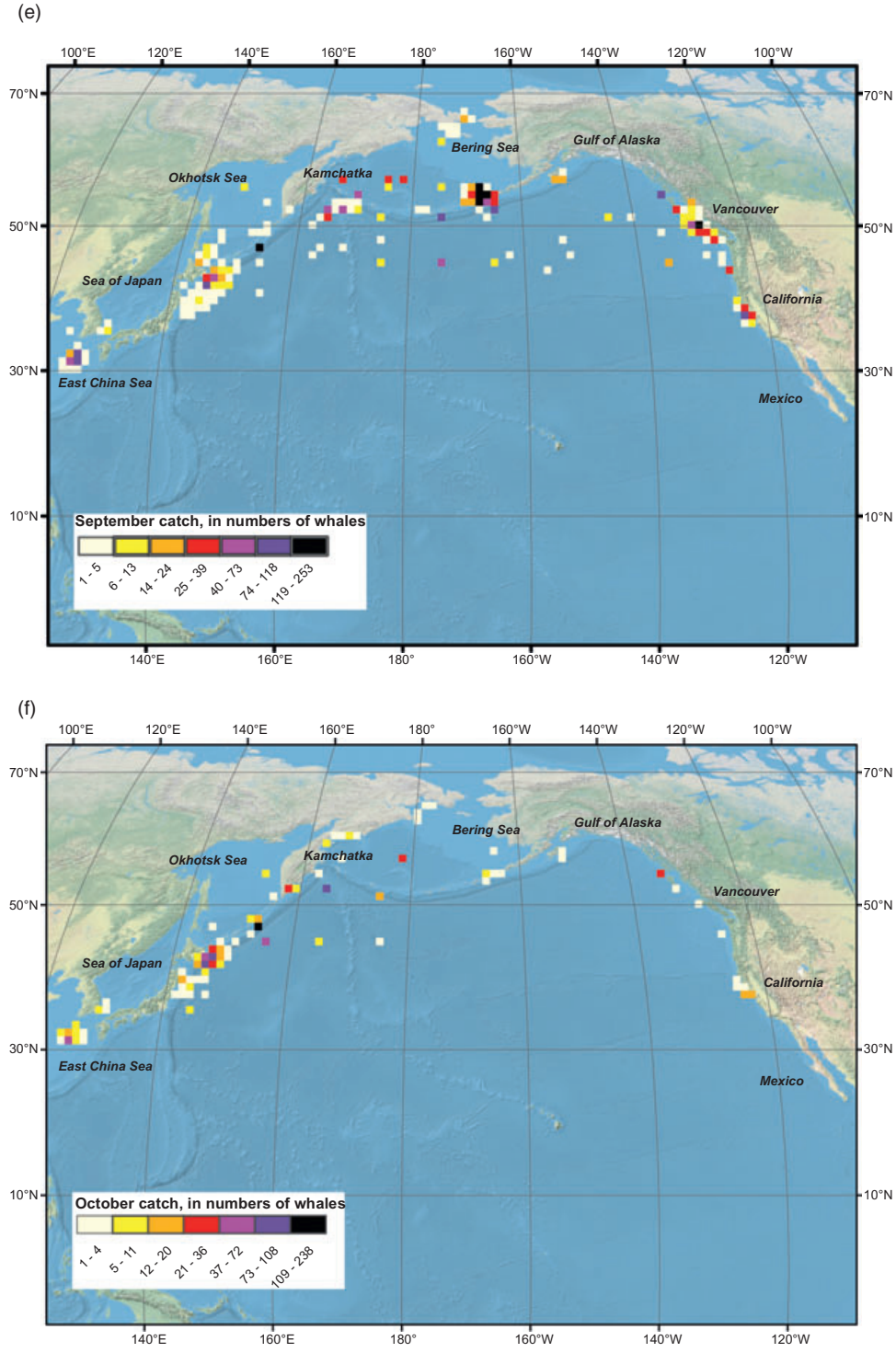

Fig. 2. (*Continued*)

fin whale as '. . . one of the numerous baleen whales that inhabit the Chukchi Sea' (Tomilin, 1937a,b; Zenkovich, 1937). He went on to state: 'This species occurs from the Bering Strait to the arctic ice edge, in the coastal zone as well as in the open sea. It migrates as far west as Proliv Longa (175 °W to 180°), Wrangel (71 °N, 180°) and Herald (71 °N, 179°W) Islands, and prefers areas free of ice, but also occurs in pools of open water among ice floes'.

Between 1969 and 1978, the crew of the catcher-boat *Zvedny*, while hunting gray whales, occasionally saw fin whales within a radius of 50 km of 67°20'N, 171°45'W, on the north coast of the Chukotski Peninsula (Votrogov & Ivashin, 1980). Many other Russian and Japanese writers have described the range of the fin whale as extending into the southwestern Chukchi Sea, without documenting any specific new records (Omura, 1955; Zenkovich, 1955; Arsen'ev, 1961; Berzin & Rovnin, 1966). However, on the latest whale sighting cruises from 1979 to 1992, no fin whales were seen in the Chukchi Sea, or anywhere north of the Gulf of Anadyr (Vladimirov, 1994).

Fin whales have rarely been documented in the eastern half of the Chukchi Sea. During extensive aerial surveys for whales in the eastern Chukchi and western Beaufort seas, from 1979 to 1987 (Ljungblad *et al.*, 1982; Ljungblad *et al.*, 1988), live fin whales were seen only once: a group of three, including a mother with a calf, directly north of the Bering Strait at 67°10′N, 168°45′W on 24 July 1981. In August 1998, a stranded fin whale was reported 3.4 km northwest of the village of Wales in the Bering Strait (65°36′N, 168°5′W). A fin whale was seen on 2 July 2008 northeast of Cape Lisburne at 69° 13.8′ N, 165° 35.4′ during aerial surveys that were conducted in the northeastern Chukchi and western Beaufort Seas from June to November 2008 (Morse, NMML, unpublished data). No other sightings or strandings of fin whales have ever been reported from the coast of Arctic Alaska (Bee & Hall, 1956; Hall, 1981; Wynne, 1992)

Southern limits

In the western North Pacific, Japanese shore stations took many fin whales during the summer months (April to November) around the southern Kuril Islands and Sakhalin, and off the north and east coasts of Hokkaido and the east coast of northern Honshu (these are areas 2, 3, 4 and 5 of Kasahara, 1950; Appendices S3 and S4). To the south of these areas, very few fin whales were taken in the summer (Kasahara, 1950; Mizue, 1950).

In most of the North Pacific Ocean, the southern boundary closely approximates the Subarctic Boundary, as defined by Favorite, Dodimead & Nasu (1976). The Subarctic Boundary is the convergence zone between the Subarctic and North Pacific currents; in most of the central Pacific, it usually lies at about 42 °N. As the Subarctic Current approaches the North American coast, it splits at about 42 °N, approximately the latitude of the Oregon-California boundary in the USA. The northern branch flows anti-clockwise around the Gulf of Alaska, and constitutes the Alaska Gyre. The larger southern branch of the Subarctic Current continues south-southeasterly as the California Current; as it flows southward, it becomes warmer and more saline because of insolation and evaporation, and the boundary between it and the warmer water to the west rapidly dissipates.

The southern boundary of the summer range of fin whales in the eastern North Pacific is deflected much farther south in the cool California Current, to about 32 °N. This is not evident in the pelagic catch data because hunting of baleen whales south of 35 °N was prohibited by IWC regulations in 1947. However, in the 1920s and 1930s, many fin whales were taken during the summer months by the catcher boats attached to the floating factories *Lansing*, *California* and *Esperanza*, when they were operating from anchorages on Catalina Island off southern California.

Farther south, off Mexico, there are almost no summer records of fin whales. On coastal cruises conducted by Rice in 1965, four fin whales were seen: one on 3 June, two on 12 June and one on 13 June, at 31°00′N, 24°35′N and 27°32′N, respectively, but none was encountered during a cruise from Mazatlan (23°11′N), Sinaloa, to the Islas Los Coronados (32°25′N), Baja California Norte, in September of the same year. The Norwegian factory ships that operated off Mexico did little whaling in May, June, July or October, and none in August and September. Their only summer catches of fin whales were single animals taken by the floating factory *Esperanza*, which took a 30 ft (9.1 m) female on 1 June 1928, a 65 ft (19.8 m) female on 17 May 1929 and a 57 ft (17.4 m) male on 30 May 1935. The male was taken off Bahia San Juanico (ca. 26°N), but available records on the other two indicate only 'Mexico's westkyst [west coast]'.

Monthly variation

Monthly catch data indicate high numbers of whale catches on both sides of the North Pacific in May and June (Fig. 2a,b; in the Gulf of Alaska and near Kamchatka-western Aleutians), and high numbers of catches in the Bering Sea/eastern Aleutian area in July and August (Fig. 2c,d). This is consistent with an eastern and western stock of whales moving from low-latitude wintering areas in the eastern and western North Pacific, moving through feeding areas as spring and summer progresses, and feeding in a centralized area in July and August.

In May, catches were distributed throughout the North Pacific, but catches were mostly sparse except for near the shore stations and in an area southeast of the Aleutian Islands (Fig. 2a). In June, catches were concentrated off Kamchatka, north and south of Unimak Pass in the Aleutians, and in the Gulf of Alaska (Fig. 2b). By July, catches were concentrated in the Unimak Pass area in the eastern Aleutian Islands and southern Bering Sea (Fig. 2c). In August, catches were spread along the Bering Sea shelf edge, all the way to Cape Navarin (Fig. 2d). In September, catches were concentrated at Unimak Pass, the Vancouver Island shore station and the Kuril Islands (Fig. 2e), and by October, catches were sparse except for near the Kuril Island shore station and in coastal Japanese waters (Fig. 2f).

Distribution of fin whales has also been plotted using POP sighting data from vessel and aerial surveys and opportunistic sightings collected from 1958–2001. The POP sighting data are more limited in geographic coverage and cover a different range of years than the catch data, and sample sizes were small in most months (less than 150 sightings in total); however, both catch and sighting data sets show similar concentration areas and monthly variation in northerly waters during the summer months (Fig. 3a). In May, most of the sightings were in the Gulf of Alaska, but there were also some sightings off California and Oregon. In June, most of the fin whale sightings were in the Gulf of Alaska and Bering Sea, but there were also some sightings off Baja California from cruises conducted by Rice in 1965. In July, there were fin whale sightings in the Gulf of Alaska and Bering Sea, and what appears to be a large concentration of sightings in Bristol Bay in the Bering Sea. In August, there were fewer sightings in the Gulf of Alaska. Sightings in September and October were in similar locations, with fin whales seen in the Bering Sea along the shelf edge, in the Gulf of Alaska, and along the US coast, but one whale was seen farther south (off Baja California) in October.

The fin whale was the most common large cetacean species seen during directed surveys in the central and eastern Bering Sea in 1999 (5 July–5 August) and the southeastern Bering Sea in 2000 (10 June–3 July; Moore *et al.*, 2002). Fin whales were seen consistently and predictably during US Fish and Wildlife Service surveys in the vicinity of Kodiak, in the Gulf of Alaska, every month of the year except for December and January, when the surveys were not conducted.

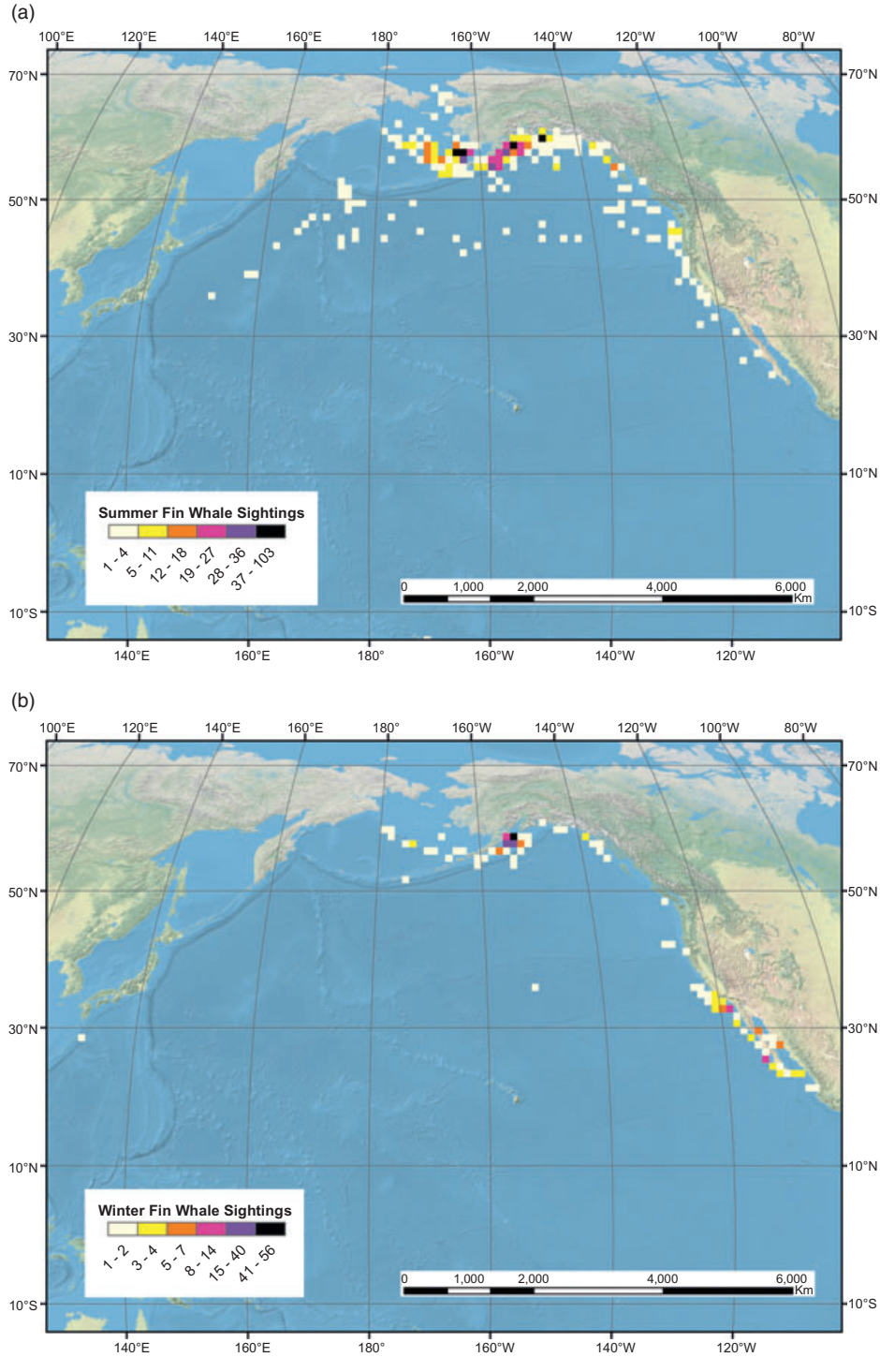

Fig. 3. Fin whale sightings from 1958 to 2001, summed by 1° × 1° square (panel). (a) Summer sightings (May–October) ($n = 1091$). (b) Winter sightings (November–April) ($n = 328$). Source: NMML Platforms of Opportunity Data (1958–2000), NMML/NMFS unpublished data, Kodiak NWR unpublished data.

Sighting surveys were conducted in the North Pacific by Japanese scouting vessels from 1964 to 1990. From May to September, extensive surveys conducted in the Kamchatka, Bering Sea and Gulf of Alaska grounds showed patterns similar to the catch data, including high densities in June both off Kamchatka and in the Gulf of Alaska, and an increase in densities in the northern Bering Sea in August. In October, in surveys conducted in the Sea of Japan and off the Japanese islands, no fin whales were found (Miyashita *et al.*, 1995).

Sightings surveys conducted by personnel at the Southwest Fisheries Science Center confirmed the presence of fin whales off the California, Oregon and Washington coasts during summer and autumn (Barlow, 1994, 1995; Forney, Barlow & Carretta, 1995; Barlow & Gerrodette, 1996), but there were no confirmed fin whale sightings during a winter aerial survey in 1991 (Forney & Barlow, 1993). Forney & Barlow (1998) confirm that fin whales were significantly more abundant in California waters during summer months than during winter months.

Winter range

It is difficult to infer winter (November to April) distribution of fin whales based on whaling records, because there are only 948 records of winter fin whales catches in the IWC catch database. Most of these are records of fin whales caught in April (742), a transitional winter/spring month. There was never any pelagic whaling during the winter months.

On the western side of the Pacific Ocean, fin whales were caught near shore stations in winter but data from many of the early Japanese shore stations are not georeferenced and are not in the IWC catch database (Appendices S3 and S4). Kasahara (1950) reported a very small catch of fin whales in winter months only (peaks in March and April) from 1911–15 in the Sea of Japan near Usetsu (Area 10 in Appendix S3). The catch in 1911 totalled 61 whales; an unknown number of fin whales were caught from 1912–14; 11 fin whales were caught in 1915; 2 fin whales were caught in 1919, and no other fin whales catches were reported in this area until 1949, the last year reported in his paper (Appendix S4).

Kasahara (1950) and Mizue (1950) reported that from 1916 until the mid-1930s, 100 to 200 fin whales were caught annually in the southern Sea of Japan, off the east coast of Korea, and in the Yellow Sea off the west coast of Korea (Areas 11 to 16 in Appendices S3 and S4). Fin whales were taken during every month of the year in these waters, but mainly during the winter months (Mizue, 1950).

Based on the timing and distribution of these catches, it is possible that these whales came from a non-migratory population in the Sea of Japan (see later section on Discovery marks).

Off the eastern (Pacific) side of Japan, there were very few winter catches of fin whales; almost no catches took place south of about 33 °N off southern Honshu, Shikoku and Kyushu.

Some fin whales were caught during winter months off Kodiak Island (Alaska) and Vancouver Island (Canada), but most of these catches were in April, a transitional winter/spring month. POP sighting records during the winter months (Fig. 3b) show that fin whales are distributed from the Bering Sea down to California. Data from November show sightings around Kodiak Island and in the Shelikof Strait area between Kodiak and the Alaska mainland. There were also sightings off southern California. In December, there was one sighting in the Bering Sea and the others were along Baja California and the Gulf of California. Fin whales were seen off Baja California in January and February, in the Bering Sea in January and February, and there was one sighting around the Aleutian Islands near Adak in February. In March, fin whales were still seen off Baja California and in the Bering Sea, but were also reported off California and Oregon, and were beginning to concentrate around Kodiak. In

April, fin whales were seen all along the US and Canadian coasts and in the Gulf of Alaska. They were concentrated around Kodiak, and were also seen in the Bering Sea.

Moore *et al.* (1998, 2006), Watkins *et al.* (2000) and Stafford *et al.* (2007) examined acoustic data for fin whale calls monitored at various sites throughout the North Pacific. At most stations, fin whale calls were produced most frequently during the winter months (December to February), and almost ceased during mid-summer (June and July). This pattern was similar in the northwestern, north-central and northeastern North Pacific (40 °N-55 °N, 150 °E-120 °W) as well as the southeastern North Pacific (25 °N-40 °N, 150 °W-120°W). In an area centred just south of the eastern Aleutian Islands, calls were most commonly recorded in July (Moore *et al.*, 1998), and in the Gulf of Alaska, where fin whale calls were detected year-round, call numbers increased from July to a peak from October to December and then tapered off until March (Stafford *et al.*, 2007). The annual pattern may primarily reflect a strong seasonal variation in the numbers of calls produced by fin whales, rather than variations in the numbers of whales occurring within range of the hydrophones. Watkins *et al.* (2000) indicated that the midwinter call sequences 'appeared to function as male breeding displays'. In studies conducted in the Gulf of California, Croll *et al.* (2002) indicated that only male fin whales produce long, patterned low-frequency vocalizations. Because such displays are probably seasonal, being tied into the presumed winter mating period of this species, their absence at other times is probably not informative with regard to the actual distribution of fin whales.

Northern limits

The conventional view is that fin whales desert their summer feeding grounds and shift to low latitudes for the winter months, although this was based primarily on equivocal observations made in the Southern Hemisphere (Mackintosh & Wheeler, 1929; Mackintosh, 1965). In the North Pacific, almost no whaling was conducted from November to May on the higher-latitude grounds. While it is likely that a scarcity or lack of whales was at least partly the reason, shorter days plus the much greater frequency of high winds and rough seas in the winter also played a major role in setting the whaling seasons. For the same reasons, whale sighting cruises in northern waters have been uncommon during the winter months. However, contrary to expectations, there were a number of sightings of fin whales in northerly waters during the winter.

According to Zenkovich (1937), fin whales are seen year-round off the Commander Islands (north of 54 °N, west of 168 °E). In January 1963, a group of 20 fin whales was seen in the Gulf of Alaska at 58 °N, 148°03′W by the crew of a Soviet research vessel (Berzin & Rovnin, 1966). Fin whales are present during winter months around Kodiak Island in the Gulf of Alaska. Especially large concentrations occur during February, April and November, which in part may be due to the increased survey effort in winter months for ongoing winter seabird surveys. Fin whales are also present in the adjacent Shelikof Strait during winter. The Shelikof Strait is dominated by the Alaska Coastal Current which provides a tremendous vehicle for nutrient mixing and foraging opportunities for many marine species (Incze, Siefert & Napp, 1997). Prey presence and distribution is probably the reason for the presence of fin whales in the Shelikof Strait waters during the winter months. Acoustic detections also confirm the presence of substantial numbers of fin whales north of 40 °N throughout the winter months. Notably, fin whale pulses were detected year-round in the Gulf of Alaska; most calls were detected from August to February (Moore *et al.*, 2006; Stafford *et al.*, 2007).

Although it has been shown that substantial numbers of fin whales may be found in higher latitudes all winter, it has not been demonstrated that any individual whales stay there

year-round. There are no sightings of fin whales with small calves during the winter months, so there is no direct evidence that high-latitude areas are used for calving.

Southern limits

Published sighting records of 'fin whales' in warm-temperate and tropical waters are all suspect because Bryde's whales *Balaenoptera edeni* or *brydei* can be mistaken for fin whales. One instance is the report by Berzin (1978) of many 'fin' and 'sei' whales seen during the American/Soviet marking cruise of the catcher *Vnushitelnyi* in the tropical eastern Pacific in 1975; Rice (1979) identified all of these animals as Bryde's whales. He also found that Berzin spent almost no time on watch on the bridge, but simply accepted the observations of the crew members, who, it turned out, were unaware of the existence of Bryde's whales.

From December to April, on the eastern side of the North Pacific, Rice found many fin whales from 35°30′N off the Big Sur coast of California south to 21°25′N off the coast of Nayarit, Mexico. The greatest numbers were encountered west of the Channel Islands off southern California. The factory ships operating off the west coast of Mexico between 1913 and 1935 reported taking only four fin whales between December and April. Rather than indicating a scarcity of fin whales, these low catches could be due to the abundance of blue and humpback whales, which were easier to catch. The POP data contain few if any convincing reports of fin whales in lower latitudes during the winter, even though the POP database includes many sightings of other species in lower latitudes during winter months.

From the western North Pacific, Japanese shore stations took substantial numbers of fin whales during all months from September to May in the southwestern Sea of Japan off the east coast of Korea, in the Korea Strait, and in the Yellow Sea off the west coast of Korea [Areas 10, 11, 12, 13 and 14 of Kasahara (1950) (Appendix S3). To the north of this region, only a few fin whales were taken from December to March (Kasahara, 1950; Mizue, 1950)].

The pelagic waters across the Pacific between the western and eastern winter grounds have yielded almost no sightings of fin whales. In the Hawaiian Islands, Shallenberger (1981) reported a stranding at Kohakuloa, Maui, in the 1950s, and a sighting north of Oahu in May 1976, but provided no further details. Rice encountered one animal in the Kauai Channel (21°24′N, 158°23′W) on 16 February 1979. Berzin & Rovnin (1966) reported some whales at 37 °N, 138 °W in February 1964. K. C. Balcomb (Center for Whale Research, Friday Harbor, WA, USA) saw 8 to 12 individuals at 17°54′N, 158°48′W on 20 May 1966 (Rice, 1974) which is rather too late for 'wintering' animals.

Based on data received by two fixed underwater hydrophones from December 1978 to April 1981 near the northernmost point of Oahu, Hawaii, Thompson & Friedl (1982) found that fin whale sounds were recorded most often from December to February, with a somewhat lower peak in August and September; none was recorded from May to July. Mobley *et al.* (1996) report a fin whale sighting off Kauai, Hawaii, in February 1994, and McDonald & Fox (1999) presented methods developed to estimate fin whale population density near Hawaii using one of the same hydrophones that Thompson and Friedl used; they confirmed that recent seasonality in call detections was similar to that detected in the Thompson and Friedl study, although fin whale calls were detected during only 12.5% of the recordings.

Calving areas

The sizes of foetuses carried by fin whales taken during the summer months demonstrate that most calves must be born during the winter months (Rice, unpublished data); similar assumptions are made about Southern Hemisphere fin whales (Mackintosh & Wheeler, 1929; Laws, 1959). However, we know of only one location in the North Pacific where calving has been

documented in lower latitude waters during the winter months. Rice has observed many fin whales during the winter months in the waters off Mexico and California, but encountered only four adults accompanied by young calves, all in either late February or early March 1965, at locations ranging from 23° to 32 °N and 109° to 117 °W. This contrasts with his experiences with gray *Eschrichtius robustus*, humpback and Bryde's whales, which were regularly accompanied by neonates in those same waters.

Movements of individual whales

In all, 965 Discovery marks were fired into fin whales, and 214 marks (23.8%) were subsequently recovered (Table 2). In 16 cases, Discovery marks were found long after the whale's carcass was processed, so reliable locations and dates of recovery were available for 198 individuals for subsequent analyses of seasonality and movement (Appendix S6). The sex of 164 of the 198 whales was reported. Fin whales were marked during 10 different months, and recovered mostly during the whaling season; 183 of 198 marking events, and 197 of 198 recoveries, occurred from May to September. Most of the marking was conducted in the Bering Sea, near the eastern Aleutians and the Gulf of Alaska (Table 2), and the majority of the recoveries were in those areas. The United States was the only whaling nation which had a programme to mark whales during the winter months (November–February) in low latitudes, and all of the recoveries of these whales occurred during the whaling season from May–August.

Movements of whales marked and recovered within the same whaling season

Forty-two (21.2%) of the whales marked were killed during the same whaling season in which they were marked (Fig. 4). All but one of these whales were marked and recovered in the high-latitude feeding areas. Whale US-14 was marked in November 1962 off northern Baja California and killed south of the Queen Charlotte Islands in May 1963. The high proportion of recoveries within the first season reflects the fact that the seasonal movements of whalers into the whaling areas over the summer season were coordinated with the occurrence of the whales on these feeding grounds. Although many whales were recovered very near to the marking location, some whales moved substantial distances seasonally from west to east (JPN-10475: 1000 km and JPN-10773: 1891 km), east to west (JPN-9535: 2933 km) and south to north (US-14: 2434 km; Fig. 4). The median distance between the marking and recovery positions during the first season was 97 km (First Quartile: 46 km, Third Quartile: 339 km, minimum distance: 0 km, maximum distance: 2933 km).

Movements of whales recovered after the first season

There were 156 marks (78.8%) recovered at least one whaling season after marking. For these 156 marks, the median time span between marking and recovery was 3.04 years (First Quartile: 1.88 years, Third Quartile: 5.89 years; minimum time span 0.70 year; maximum 17.56 years). The shortest interval between marking and recovery was of whale JPN-6834, a male marked late in the whaling season in September in the Unimak Pass area and recovered the following May near the western end of the Aleutian chain, over 1700 km away from the marking site. The longest interval between marking and recovery was of whale JPN-151, a female marked in the Sanriku-Hokkaido area in July 1949 and killed in the same general area (less than 650 km away) almost 18 years later in February 1967. The median distance between the marking and recovery positions of whales recovered after the first season was 449 km (First Quartile: 225, Third Quartile: 889, minimum distance: 40, maximum distance: 4842 km).

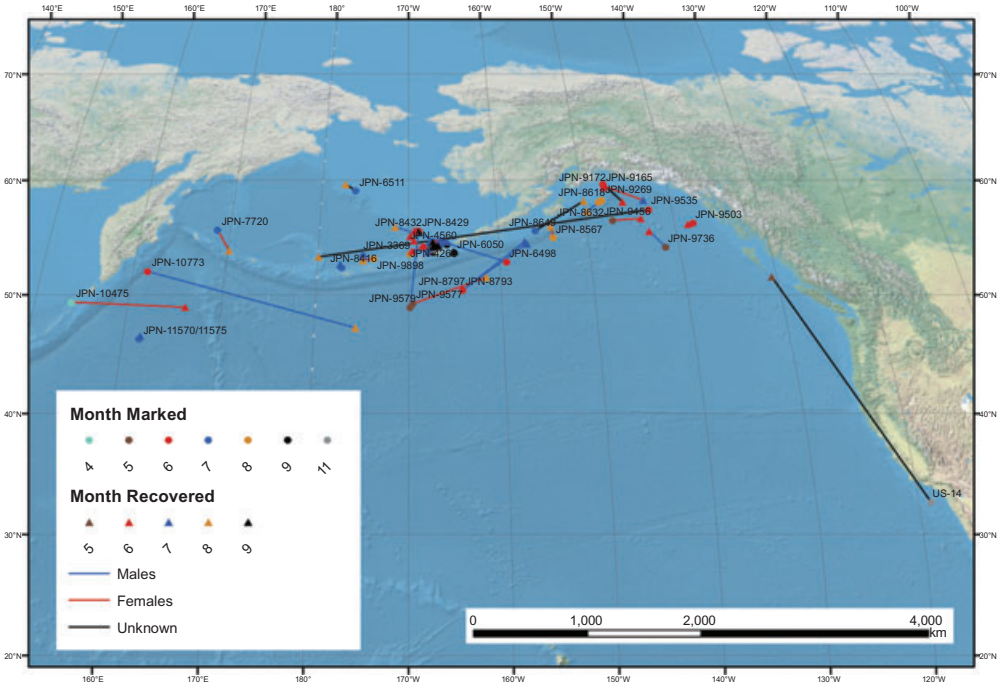

Fig. 4. Whales marked and recovered within the first season ($n = 42$). Source: Omura and Ohsumi, 1964; Ivashin and Rovnin, 1967; Ohsumi and Masaki, 1975; Rice, unpublished data.

Consistent movements

Ohsumi & Masaki (1975) noted that on two occasions, two whales that were marked together at the same time were later recovered together at the same time and place some distance from where they were marked. One set was recovered after 23 days (JPN-8793 and JPN-8797, see Appendix S7), and the other set after 5 days (not included in Appendix S6 because precise location data were not available).

The data presented here include an additional four sets of two or three whales that were marked together at one location on the summer grounds, and then recovered together at a different location at around the same time. In two cases, the whales were recovered 8–10 days or 23 days after marking (Appendix S7). In the other three cases, the whales were recovered 3–6 years after being marked (Appendix S7, Fig. 5). Also, in one of these cases, a third whale (JPN-8649) made an almost identical movement except that it had been marked 5 years later than the other two whales.

There were an additional four sets of whales which showed similar movements, but were recovered in different years. The whales in each of these sets were marked on the summer grounds within a few days of each other, and were recaptured at some distance from the marking location, at nearly the same location and at the same time of year, but 2 to 16 years apart (Appendix S8, Fig. 5). In these cases, the distances between marking and recovery ranged from over 400 km to almost 3000 km (Appendix S8, Fig. 5).

Three whales were marked on the winter grounds, two (US-616 and US-618) on the same day, the other one (US-414) nearby 3 days earlier. Two and half years later, two of them (US-414 and US-616) were recovered in summer at the same time and place, the third (US-618) close by 37 days earlier (Appendix S7, Fig. 5).

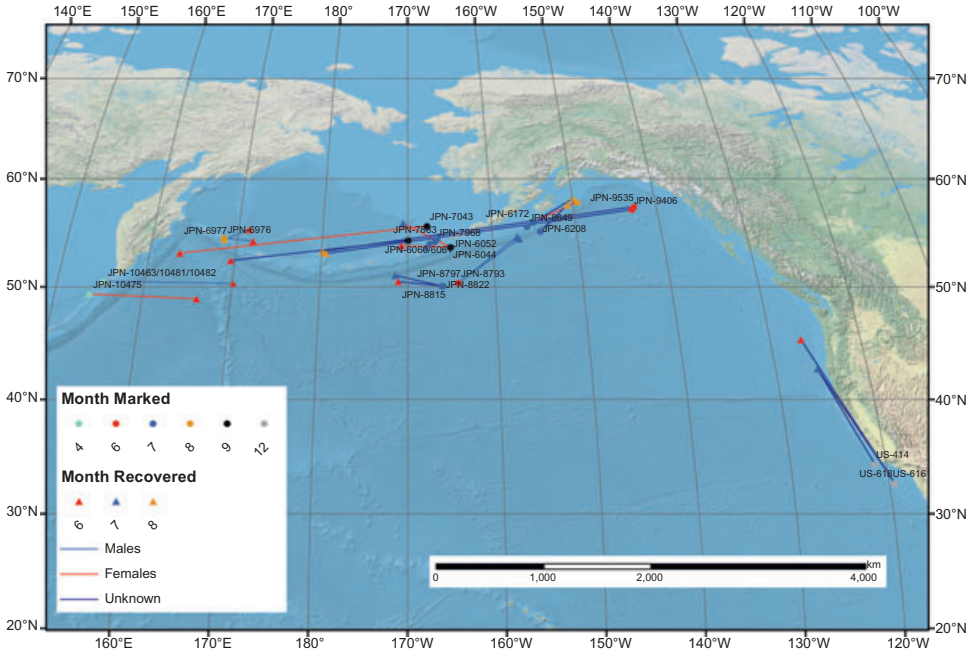

Fig. 5. Consistent movements ($n = 22$). Source: Omura and Ohsumi, 1964; Ivashin and Rovnin, 1967; Ohsumi and Masaki, 1975; Rice, unpublished data.

Some of these events may reflect long-term associations among individual whales, although the data are inadequate to assess whether the individuals concerned were socially associated at the time of marking and recovery. However, these data do suggest a tendency for groups of whales to conduct feeding migrations along similar routes, and that individual whales may exhibit seasonal as well as annual site fidelity within and between seasons, presumably as long as prey distributions remain similar.

Seasonality of mark and recovery locations

In order to explore the seasonality of mark and recovery locations independently of the number of years between marking and recovery, the number of 'season-days' between mark and recovery dates was calculated as the absolute value of the difference between the day of the year marked and the day of the year recovered. For example, whale JPN-3287/3343 (double-marked) was marked on 6 August 1954 and JPN-4658 was marked on 10 August 1954. Mark JPN-4658 was recovered on 6 July 1955 (330 days later) and mark JPN-3287/3343 was recovered on 2 July 1961 (2522 days later). However, in both cases there were 35 season-days between marking and recovery.

During much of the summer whaling season (i.e. within the first 80 season-days between marking and recovery), there is no apparent trend in season-days vs. distance between marking and recovery (Fig. 6). With the exception of a female whale which was marked near Kamchatka in May and recovered in the Gulf of Alaska in June (USSR-637: 4842.2 km), two whales marked near each other in the Gulf of Alaska in June and recovered near each other in the Aleutians in August, and two whales that travelled long distances (JPN 9406: 2881 km and JPN-9535: 2932.5 km), most whales killed within 80 season-days of marking were recovered less than 1500 km from their marking location (Fig. 6). The median distance between

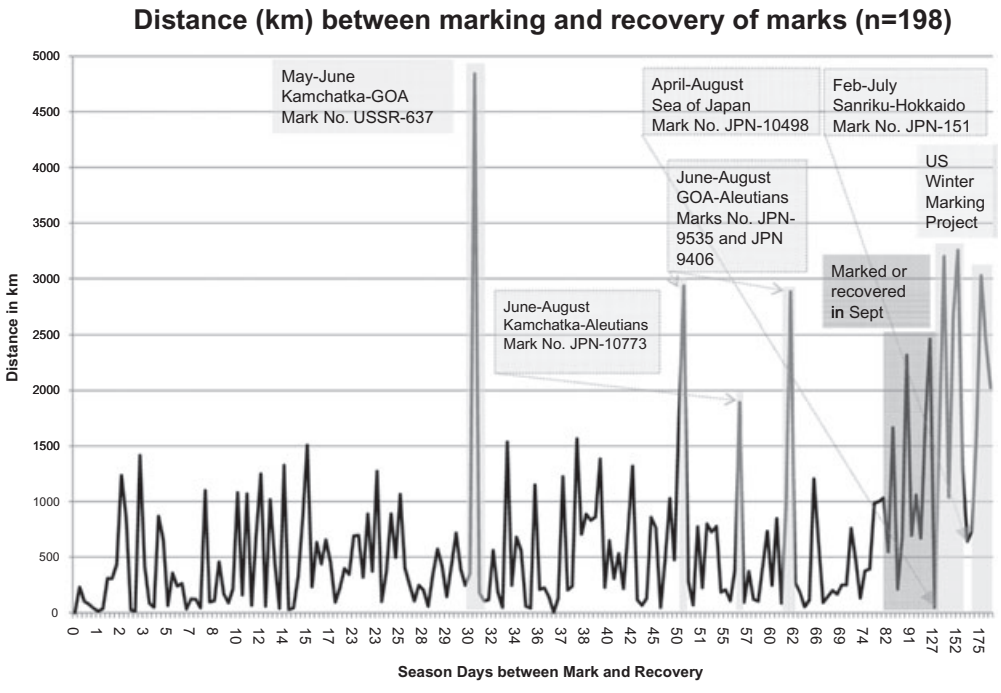

Fig. 6. Distance between mark and recovery locations by 'season-day' ($n = 198$).

mark and recovery locations of the 175 whales caught within 80 season-days from marking was 324 km (First Quartile: 123 km, Third Quartile: 732 km, minimum distance: 0 km, maximum distance: 4842.2 km; USSR-637, see previous discussion). In contrast, the median distance travelled by the 23 whales of which the marks were recovered more than 80 season-days after marking was 1600 km [Fig. 6; First Quartile: 689, Third Quartile: 2375 km, minimum distance: 46 km (JPN-10498, marked in April and recovered in August in the Sea of Japan), maximum distance: 3253.3 km; US-78, marked in January off Baja California and recovered in June in the Gulf of Alaska; Fig. 7]. Eleven of those 23 whales were marked during the winter months off Baja California, and nine were either marked or recovered in September near Unimak Pass. These data confirm seasonal migrations north from wintering areas off Baja California to feeding areas along the US west coast and Gulf of Alaska. In addition, Unimak Pass appears to be a concentration area for fin whales in September.

Two of the 'out-of season' recoveries were marked and recovered in Japanese waters, one in the Sea of Japan and the other off Sanriku-Hokkaido, indicating the possible existence of non-migratory stocks in these areas. One (JPN-10498) was recovered after 127 season-days about 46 km from the marking location; the other (JPN-151) was recovered after 166 season-days 642 km from the marking location (Figs 6 and 7). Numbers of recoveries of whales marked in Japanese waters were low, and none of these recoveries documented long-distance movements to any of the other whaling grounds. This further supports the hypothesis that one or more non-migratory stocks exist that do not migrate to northern waters where the catch effort was much higher, but could also be explained by movements to areas where extensive whaling was not occurring. However, the small sample size constrains a detailed evaluation of these hypotheses.

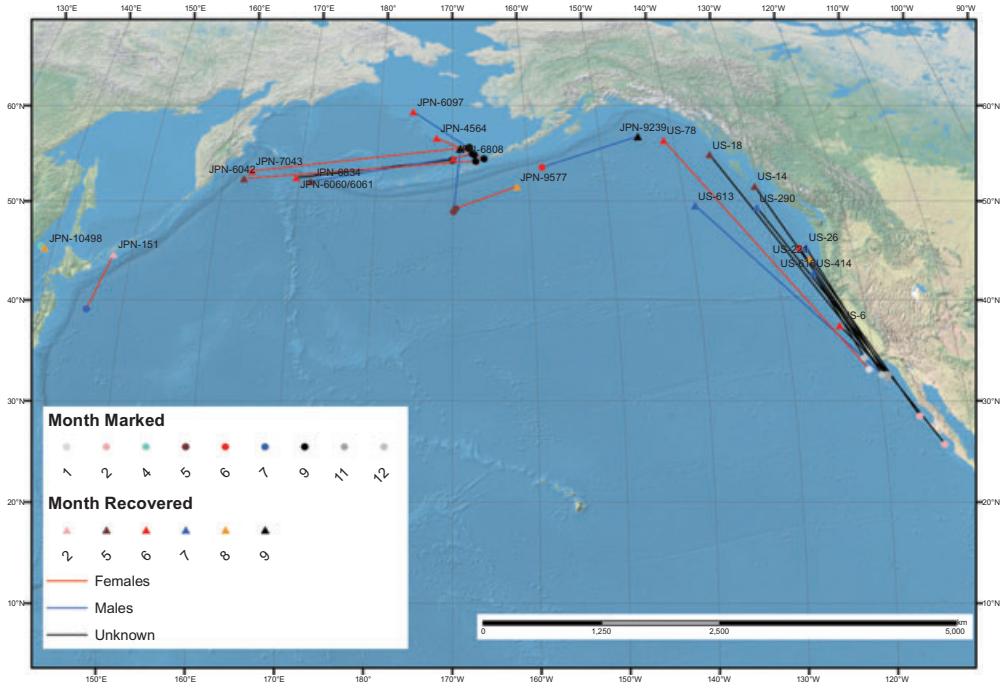

Fig. 7. Recoveries more than 80 season-days ($n = 23$). Source: Omura and Ohsumi, 1964; Ivashin and Rovnin, 1967; Ohsumi and Masaki, 1975; Rice, unpublished data.

CONCLUSIONS

Fin whales may be found throughout the entire North Pacific from the southern Chukchi Sea south to the Tropic of Cancer. Our distributional and mark-recovery data agree with early immunogenetic findings which suggest that the population is segregated into two major demes with separate winter mating grounds: one in the western and one in the eastern North Pacific. During the summer, at least some members of these two demes probably mingle in the Bering Sea-Aleutian Islands area. This corresponds with findings based on Antarctic marking data which suggested that fin whales from different Southern Hemisphere winter grounds intermingle on the higher-latitude feeding grounds (Brown, 1954, 1959, 1962).

During summer (May to October), fin whales are found throughout the North Pacific, from the southern Chukchi Sea south to the Subarctic Boundary and the southerly reaches of the California Current. Catch densities and movements based on Discovery-mark recoveries show that individual whales may disperse longitudinally, some moving all the way from Kamchatka to the Gulf of Alaska, or vice versa, as the season progresses. It also appears that whales which moved from both the eastern and western North Pacific tend to concentrate in the Bering Sea-eastern Aleutian Islands area in July and August, and to move north in the Bering Sea along the shelf edge as the ice recedes in late summer.

Some mark recoveries suggest that individual whales may follow the same routes and schedules in successive years, which indicates the possibility of predictable migrations and seasonal site fidelity to specific summer feeding grounds.

Perhaps because they are fast swimmers, fin whales appear to be capable of rapid long-range movements, possibly to take advantage of widely dispersed prey concentrations. At least in the past when stomach content data were collected by whaling operations, fin whales

in the western North Pacific appeared to switch prey from krill to fish as they moved north along the shelf edge in the Bering Sea and through the coastal waters of the Kamchatka Peninsula, presumably as the ice edge receded during the summer months. Based on median distances between marking and recovery locations within the whaling season, it appears that fin whales typically travel 200–800 km while foraging.

In winter (November to April), it has been assumed that the bulk of the North Pacific population disperses southward toward the Tropic of Cancer, where mating and calving are presumed to take place, but specific low-latitude wintering areas remain undiscovered for the migratory whales. Coastal whalers took fin whales regularly during all winter months around Korea and southern Japan, and whales have been seen regularly during winter in the waters off southern California and Baja California. North of 40 °N there are numerous fin whale sightings and acoustic detections during winter months.

Fin whales are seen predictably and regularly in winter months in the Kodiak region of the Gulf of Alaska, and some of the earliest winter surveys off the Commander Islands documented fin whales year-round. We cannot currently say whether these northern observations indicate: (i) that some individuals remain year-round on feeding grounds; (ii) that some whales undertake very short migrations in winter before returning north; and/or (iii) that the population structure of fin whales is more complicated than a simple migratory-movements model would suggest, so that varying patterns of occurrence and seasonal distribution are exhibited by different sections or classes of the population(s).

There is good evidence from genetic and other data for the existence of discrete, non-migratory stocks of fin whales in the Gulf of California and in the East China Sea. Marking and seasonal catch data from the Sanriku-Hokkaido and northern Sea of Japan areas indicate the possible existence of additional non-migratory stocks of fin whales, but sample sizes are very small and further investigations must be conducted. Additional research is needed to answer key questions, including:

1. Where are migratory fin whales concentrated during the winter months? Are they distributed throughout the North Pacific, or are most of them in the waters immediately off the American and Asian coasts? Do they migrate to any particular areas to mate and calve? Extensive sighting, acoustic and satellite tagging studies could address these questions.

2. Do fin whales show site fidelity or philopatry to any particular areas? Although the Discovery mark data presented in this paper suggest habitat usage patterns, there are no other longitudinal data on North Pacific fin whale habitat use within or between seasons. Satellite tracking and photo-identification studies of individual whales could address these questions.

3. Are fin whale populations on the eastern and western winter grounds genetically differentiated? Are there two or more migratory stocks of fin whales in the North Pacific? Can the existence of additional non-migratory stocks in the waters near Japan and Korea be confirmed? Biopsy samples should be collected so that molecular genetic analyses can be performed to answer these questions.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Fin whales killed by the main whaling nations between 1911 and 1985 and reported to the IWC.
Appendix S2. Coastal whaling operations in the eastern North Pacific, and years for which monthly catch-per-unit-of-effort are available.
Appendix S3. List of areas and numbers of shore stations in the western North Pacific from 1911 to 1949 (from Kasahara, 1950; Mizue, 1950).
Appendix S4. Japanese shore station catches of fin whales for the years 1911–49 (from Kasahara, 1950).
Appendix S5. Fin whale sightings by year and month [National Marine Mammal Laboratory's POP database (1958–2000), NMFS unpublished data, Kodiak NWR unpublished data].

Appendix S6. Discovery mark recoveries where mark and recovery locations were reported.
Appendix S7. Persistent associations of whales marked at around the same time and caught near each other at around the same time.
Appendix S8. Seasonal movements to the same feeding areas in different years.